TERRITORY AND SONG IN THE LEAST FLYCATCHER

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DURING the summers of 1942, 1944 and 1946, I made an intensive study of the Least Flycatcher, *Empidonax minimus*, in the vicinity of Douglas Lake, Cheboygan County, Michigan. My study covered a total of 44 nests: 19 in 1942 and 14 in 1944 on an area of 7 acres of broken aspen woods (i.e., woods in which there were several houses, roads and paths) within the Biological Station camp grounds; and 11 in 1946 on the same 7 acres plus 14 adjacent acres of unbroken aspen woods (i.e., woods without houses, roads and paths).

TECHNIQUES

The study area was systematically searched for nests, which were numbered approximately in the order found. Their position and the territorial boundaries of the nesting pairs I have indicated on maps for the three years studied (see maps).

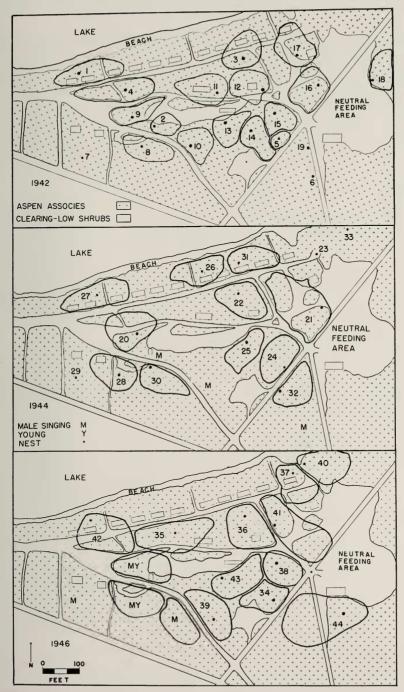
Nests 1, 2, 3, 4, and 5 were observed for a total of 165 hours between June 20 and August 3, 1942. Nests 17 and 21 were observed for 30 hours between June 27 and July 15, 1944. Platform blinds were placed level with, and 3 to 5 feet from, these nests. Song perches and territorial boundaries of 14 pairs with nests were plotted in the field during 40 hours of observation between June 24 and August 3, 1946. Morning song was studied on ten trips, each of which began about an hour and a half before sunrise and ended when rhythmic singing ended. Throughout my study the time recorded was Standard Time. Observations outside of the blinds were made with an 8x binocular and a 32x telescope.

The females of Nests 2, 4, and 21 were marked with aluminum bands colored with nail varnish, and the female of Nest 21 was made more readily identifiable by cementing a yellow feather to her upper tail coverts. Each of these four birds was captured in a quarter-inch mesh wire trap built around the nest. The hinged, propped-up top of the trap was released by a string from the blind as soon as the bird settled on the nest. The sex of unmarked birds could sometimes be recognized through their call notes and songs. A few individuals could be recognized as such by special mannerisms or details of coloration.

HABITAT AND POPULATION

The study area was largely second-growth woodland. Large-toothed aspens (*Populus grandidentata*) and quaking aspens (*P. tremuloides*) dominated, but there was a scattering of birch (*Betula papyrifera*), maple (*Acer rubrum*), and

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Distribution in 1942, 1944 and 1946 of Least Flycatcher nest-territories and nest-sites at the University of Michigan Biological Station. Note that in 1944 and 1946 certain singing males were not on territories.

pine (*Pinus resinosa*). The crowns of the large-toothed aspens formed a canopy 30 to 40 feet high. A lower leaf-stratum was composed of the tops of birch, maple, and quaking aspen saplings. The ground cover was primarily bracken (*Pteris aquilina*), under which a few shade-tolerant plants grew. Fire had destroyed the original forest in 1901.

The 7-acre area had a population density of 2.7 and 2.0 pairs of Least Flycatchers per acre, respectively, in 1942 and 1944. The birds seemed to like the constant human activity and the artificially open woods; farther away, where the aspen woodland was unbroken, they were much less common. The 14-acre area had a population density of 0.7 pairs per acre in 1946.

Censuses of bird populations respectively in aspen, beech-maple, and pine communities in Cheboygan County have revealed that the Least Flycatcher inhabits only the aspen and beech-maple associations. Prescott (1946) found

TABLE 1
POPULATION DENSITY IN LEAST FLYCATCHER BREEDING HABITATS

Authority	Habitat Type	Years	Number of Acres	Total Pairs Counted	Average Per 100 Acres	
Saunders	Orchard and shade trees	1930-31	50	6	12	
Saunders	Aspen-cherry forest, undisturbed	1930-31	1166	43	3.7	
Saunders	Aspen-cherry forest, cleared for camping	1930-31	123	4	3.3	
Saunders	Aspen-maple thicket	1930-31	333	7	2.1	
Hofslund	Beech-maple forest	1946	160	9	5.6	
This paper	Open aspen woods	1942	7	19	271	
This paper	Open aspen woods	1944	7	14	200	
This paper	Open aspen (7 acres) plus closed aspen (14 acres)	1946	21	11	52	

one Least Flycatcher in a pine community. It was singing along the border of a small island of aspens within the pine forest. Saunders (1936) encountered the Least Flycatcher in 4 out of 19 habitats that he censused in Allegany State Park, New York. An analytical summary of Least Flycatcher population data is given in Table 1.

Whereas neither Saunders nor Hofslund (1946) found as great a density of population as I did, their figures do demonstrate the Least Flycatcher's preference for open woods. Saunders found the greatest density in orchards and among shade trees—decidedly the most open of the habitats—and the smallest population in the aspen and red maple thicket—the least open habitat. Hofslund found that the species did not invade the forest interior but kept to the edges of the paths and roads crossing his study plot. We are forced to conclude, therefore, that open areas in the woods are a primary habitat requirement, and that trees of many sorts are suitable so long as there are openings among them. Forbush (1927:361) states that the species has "become accustomed to man

and his works and prefers his neighborhood to more retired localities." Nearness to human habitations can hardly be considered a habitat requirement, however; the important feature of the human neighborhood is probably the man-made openings in the woods.

This preference for edge was clearly shown by the sites of the 44 nests I studied: 20 were on the edges of clearings or along roadsides; 18 were less than 10 feet from such an edge; and 6 were slightly more than 20 feet from the edge. The preference seems to be based on two requirements: shade for the nest, and an open area for feeding and for song posts.

I found that the larger open areas surrounding the woods (e.g., the saw mill clearing and the dump area) were used as neutral feeding grounds by all the Least Flycatchers which nested nearby. The availability of such an extensive neutral feeding ground may decrease intraspecific conflict and the size of individual territories, hence increase population density.

All territories included, or were bordered on at least one side by, an opening in the woods. The song posts used early in the morning were on these edges, and although the male moved about the territory during the singing period, most of the singing itself was done from the edge.

INTERSPECIFIC HABITAT RELATIONSHIPS

So segregated in their several niches were the various bird species of the area that I observed little evidence of interspecific competition. At Nest 21, a Chipping Sparrow (Spizella passerina) built its nest in the same maple tree, yet the two species lived together quite amicably. Four flycatchers—the Phoebe (Sayornis phoebe), Kingbird (Tyrannus tyrannus), Wood Pewee (Contopus virens) and Crested Flycatcher (Myiarchus crinitus)—nested and fed in areas immediately adjoining Least Flycatcher territories and sometimes briefly invaded them, but I observed no conflict. Williams (1936:382) commented on the interspecific ecological segregation of the breeding Acadian Flycatchers (Empidonax virescens), Wood Pewees, and Crested Flycatchers of a beechmaple climax community. "So far as food habits are concerned the flycatchers form a group by themselves, each species having its own hunting ground."

At first glance the Redstart (Setophaga ruticilla) and Least Flycatcher appear to occupy precisely the same habitat niche. The nest of the one resembles that of the other in site and structure. Yet Hofslund (1946) reported the nesting of the two species side by side without conflict in a beech-maple forest near Douglas Lake. He found, however, that the more abundant Redstart (38 pairs per 100 acres) nested throughout the woods, whereas the Least Flycatcher (6 pairs per 100 acres) nested only along paths and roads. Within my study area no Redstarts nested. The species seemed to prefer the dense, continuous maple forest farther away from the Biological Station.

I observed only one instance of interspecific conflict—that between a pair of nest-building Cedar Waxwings (Bombycilla cedrorum) and a pair of Least

Flycatchers whose nest contained eggs. The encounter took place on July 27. 1944. The flycatchers' nest was outside my study area, but on the Station grounds. I watched developments for 35 minutes, during which period the waxwings made three visits to the nest, stealing material each time. When they appeared in the vicinity both the male flycatcher, perching 50 feet from the nest, and the female, sitting on the nest, called rapidly; but not until the robbers began to tear at the nest did the male actually attack. He darted at their heads with bill snapping, hovered over them, and fluttered about them calling excitedly. The female remained on the nest, pecking at the waxwings and calling too, but she did not leave even though the whole structure rocked beneath her. The waxwings evinced little concern over the noise and attacks. Finally, on their third visit, the female flycatcher left the next when it began to tip over. Both flycatchers now flew at the waxwings, causing them to retreat momentarily. The end came when one of the waxwings pulled so much of the nest away that the three eggs and torn remains fell to the ground. Both flycatchers made a final assault, but when the waxwings flew off they carried pieces of the nest in their beaks.

What impressed me most about this fight was the failure of the male fly-catcher to attack the waxwings when they first appeared in the vicinity of the nest. I was impressed, too, with the refusal of the female to leave her nest until the very last. Davis (1941:160) has said of the Kingbird that "the important characteristic of this interspecific fighting is that only the male fights." I have never witnessed an encounter between Least Flycatchers and a nestrobbing Blue Jay (Cyanocitta cristata), but I suspect that in cases of that sort, involving a considerably larger bird species or predatory mammal, both the male and female would instantly attack. Certainly, as I have many times observed, when a human being interferes at the nest both the male and female attack with swoops and bill-snapping and the attack does not cease until the human being has withdrawn.

TERRITORY

Within its chosen habitat, the Least Flycatcher selects and defends a territory in which it spends much of its time, builds its nest, and gathers some food for itself and young. Beyond the borders of this territory it may use a neutral feeding ground, where individuals of both sexes feed without conflict.

The breeding cycle of the Least Flycatcher covers about 50 days. Nest-bui ding requires about 5 days, egg-laying 3 to 6 days, incubation 15–16 days, fledging 14 days, and feeding of full-fledged young about 10 days. The earliest date on which I actually saw an active nest was June 19 (the nest held two young about three days old on that date). This nest must have been built in the last part of May. The latest date on which I found a nest under construction was June 24. The first nest of this pair had been destroyed. The female builds the nest, incubates the eggs, and broods the nestlings. Both sexes feed the young.

The male remains within the nesting area throughout nest-building, egglaying, and incubation except when he visits a neutral feeding area. Occasionally he feeds the female while she is on the nest. I noted the following behavior at Nest 4 on the ninth day of incubation: "A few hours after I banded the incubating bird the male came to the nest to feed the female, giving his usual guttural *speetz*. This time instead of remaining on the nest the female flew off, flying wildly about the territory with the male in chase. After a few seconds of flight the female landed on a branch ten feet from the nest where the male fed her, after which she flew back to the nest. The male remained on the branch singing for about a minute."

Each nesting pair is dominant over other Least Flycatchers in its own territory, and intrusion of a neighboring individual or pair always incites immediate reaction of defense. The boundaries of territories seem to change somewhat from time to time, but even when a nest is destroyed and a new one built the general location of the territory does not change much. The largest territory I measured occupied 0.50 acres (21,881.5 square feet), the smallest 0.03 acres (1431.5 square feet). The average of 33 territories was 0.18 acres (8036.8 square feet). The average distance between nests was about 175 feet, the greatest 215 feet, and the least 60 feet. Territories are maintained by pursuit, threat-posture, fighting, and song.

Pursuit. When a Least Flycatcher appears in a Least Flycatcher territory not its own it is immediately recognized as an intruder by the resident male. The owner of the territory utters a sharp note and gives chase, both birds flying excitedly and swiftly about. If the intruder does not fly out of the territory, a fight ensues. The resident male forces the intruder to the ground, where the two posture (see below) and then engage in a tumbling struggle which ends in the retreat of the defeated bird (apparently always the intruder). After following the intruder a few feet beyond the territory, the resident male returns to a favorite perch and calls *che-bec*.

The male is usually the first to fly to the defense of the territory. The female's defense is different from the male's in some ways. First, she does not defend the entire territory but is primarily concerned with an area 20 feet in radius around the nest. She does not attack or pursue the intruder until it has come well within this restricted area; then, if her mate does not appear, she flies from the nest in pursuit. Usually when she thus leaves the nest only a pursuit flight occurs, for this is sufficient to force the trespasser out. If two birds enter the territory at the same time, the female sometimes assists the male in defense; in these cases, however, the male always is first to fly toward the enemy, the female following a few seconds later. This behavior I observed on six occasions.

Davis (1941:158) described this type of behavior in the Kingbird. "The pair which has already acquired the territory defends the area in violent fights. A most important point is that both sexes cooperate to drive out the intruder. The female fights as vigorously as the male."

Threat-posture. Threat-display involves enlarging of apparent body size by fluffing out the breast feathers; raising the crest; extending, vibrating, and bending the wings; spreading and flicking the tail up and down; and crouching. Upon recognition of an intruder in the territory the resident male flicks his tail, raises his crest, crouches momentarily, and leaves his perch in pursuit. This requires only a second or two. Following the chase both birds may drop to the ground, crouch, and face each other with outstretched, vibrating wings. When the resident male has driven the other off, he returns to a favorite perch and sings *che-bec*. Each time he sings he flicks his tail and raises his crest.

The female threat-postures only occasionally. When, in defense of territory she meets an opponent, she spreads her tail, raises her crest, and fluffs out her breast feathers. She threat-postures only briefly and does so principally in opposing man, small mammals and such birds as are actually attacking the nest.

Davis (*loz. cit.*), writing of the Kingbird, described a display which he believed "served the same ends as the territory song in many passerine birds." He stated: "The fighting consists of air battles, conducted with great chattering and display. A note *b-zee* is used in addition to the *tik* note. A great tumbling display occurs when the intruder is some distance away. . . . The bird flies high in the air chattering with wings quivering and then, after tumbling, climbs high again and repeats the tumble several times." I have seen much aerial chasing among Least Flycatchers but never a display comparable to this.

Fighting. Fighting is closely related to pursuit. Often during a chase the two birds fly at each other just before dropping to the ground. Fighting can be so swift that only a flashing of feathers and whirling of two bodies is visible to the human eye. Fighting usually follows what appear to be attempts to intimidate through posturing. Only once have I seen what I was sure was a female Least Flycatcher fighting (see discussion above of the Cedar Waxwings).

Song. Song is important in establishment and maintenance of territory. Ornithologists are in wide agreement that the song of the male sounds very much like *che-bec* (Bent, 1942:221). This *che-bec* varies little within itself as a phrase. It is repeated rapidly during part of the morning song period; in day-time singing it is repeated less regularly and not very rapidly; and in flight it is sometimes mixed with certain unmusical notes. According to my observations the male rarely sings in the nest-tree.

The morning song is given daily by the male within the confines of the territory, usually a few feet above the level of, but not very near, the nest. It is a continual and more or less rhythmical repetition of *che-bec*. It is given from several song-perches in trees along the edges of the territory. Where several nests are close together (as were Nests 34, 38 and 44) most of the singing is done along the borders of the territories. All of the males of such an area seem to sing with the same tempo and intensity, as if performing in unison. They jerk their

heads and flick their tails with each repetition of a song phrase. The females remain quietly on their nests during these joint performances.

About the time the female begins incubation the male's morning song is given from before dawn until about sunrise. It decreases in duration as the nesting cycle progresses. Nine of the ten mornings on which I paid special attention to morning song were clear. On July 18 the sky was overcast, but I could not see that this grayness of day affected the singing of the males in any way. On June 29 the very first *che-becs* sounded about 15 minutes before rhythmical singing started. At 3 o'clock (19 minutes before civil twilight), 15 males began rhythmical singing. They sang for 70 minutes, ending 14 minutes after sunrise. Morning song usually begins rather slowly in the semidarkness, increases in tempo as the sky brightens, and becomes slower again about sunrise. When sung most rapidly (as it was 30 minutes before sunrise on June 29 and July 4, in 1946), the *che-bec* is repeated about 60 times a minute. This fervent morning singing does not continue all summer. By July 15, the song

TABLE 2

Data on Least Flycatcher Morning Twilight Song in 1946

Bird	Date	Morning		First Call note		Rhythmic Song				
		Civil Twi- light Began	Sunrise	Hour	Min- utes before Sunrise	Hour	Min- utes before Sunrise	Hour Ended	Dura- tion	Num- ber of Males Singing
Least Fly-	June 29	3:19	3:56	2:45	71	3:00	56	4:10	70	15
catcher	July 4	3:23	3:59	2:50	69	3:07	52	4:05	58	14
	July 12	3:28	4:05	3:10	55	3:20	45	3:50	30	10
	July 15	3:30	4:07	3:25	42	3:30	37	4:05	35	11
	July 18	3:32	4:10	3:30	40	3:40	30	4:05	25	10
	July 22	3:36	4:14	3:30	44	3:45	29	4:02	17	4
	July 25	3:39	4:17	3:35	42	3:45	32	4:04	19	4
	July 28	3:42	4:20	3:43	37	3:45	35	4:00	15	2
	Aug. 2	3:47	4:26	3:55	31	_	-	_	-	1
Kingbird	June 29		3:56			2:20	96			
	July 4		3:59			2:30	89	3:05	35	
	July 18		4:10			3:10	60	3:40	30	
	July 22		4:14			3:12	62	3:50	38	
	July 28		4:20			3:15	65	3:55	40	
Wood Pewee	July 12		4:05	3:14	51	3:18	47			
	July 18		4:10	3:16	54	3:25	45	3:45	20	
	July 25		4:17			3:40	37			

Sunrise and the beginning of morning civil twilight, recorded here in Standard Time, were determined for 85° W. longitude and 45° N. latitude from "Tables of Sunrise, Sunset, and Twilight", Supplement to the American Ephemeris, 1946. Morning civil twilight begins when the sun is 6° below the horizon and ends at sunrise. To convert Standard Time to Eastern Standard Time, add one hour.

began at civil twilight, lasted 35 minutes, and ended 2 minutes before sunrise. By the time the young were ready to leave the nest (July 22) it lasted only 17 minutes, stopping 12 minutes before sunrise. When the young scattered from the territory it stopped altogether (see Table 2).

The cessation of morning song in late summer is a gradual process, since the pairs are at various stages in the nesting cycle. Individuals which were late in nesting in 1942 did not sing much during my period of observation. Their song period was shorter than that of males at the same stage of the nesting cycle earlier in the season when all the birds of the area were singing. Many males singing in adjoining territories seem to stimulate one another. The quality and quantity of singing, then, do not depend entirely upon the stage the individual males have reached in the nesting cycle, but also upon the number of singing males in adjoining territories. The greater the number of males the greater the need for song—i.e., for defense of territory through song. When the young scatter, singing stops. In this respect the Least Flycatcher seems to differ from the Wood Pewee. Craig (1943:153) states that "daytime singing continues long after the end of the breeding season."

Mention of the Wood Pewee leads to a consideration of the ways in which the morning song of the Least Flycatcher resembles, and differs from, that of certain other flycatchers of the Douglas Lake region. The Wood Pewee's morning song certainly is much more complex, and also more musical. It is notable for its rhythmic quality. The Phoebe has an early morning song, but I know little about it. On June 25, 1946 I heard a Phoebe start singing about an hour and a half before sunrise. It stopped at sunrise. The Kingbird begins its song even earlier than the Least Flycatcher and Wood Pewee do (on June 29, 1946, more than an hour and a half before sunrise) and usually continues 30 to 40 minutes. The song is rhythmical and the basic phrase has several syllables. It decreases in duration and intensity as the season advances (see Table 2). The Crested Flycatcher has a twilight song (Nice, 1928:255) but I did not hear it, possibly because of the lateness of the season.

Daytime Song. Daytime song is never, apparently, the routine performance that morning song is. It may be given at any time during the day. Like morning song, it is a repetition of the phrase *che-bec*. Day time singing which I heard in 1946 lasted three to five minutes after interspecific territorial disputes, and the *che-bec* phrases were uttered about 50 times per minute during these periods. Daytime song accompanies the male's approach to the female (whether she is on the nest or not); it serves as a protest to invasion of the territory by a human being; and it may serve as territory advertisement whether or not there is threat of interspecific or intraspecific dispute.

Flight Song. The flight song has been variously described. Forbush (1927: 360) says that it consists of "a jumble of notes uttered in a kind of ecstacy" while the male "flutters about in a circle." Hoffman (1904:202) says that just before dusk the male, after flying up from a tree near the nest, sings a song in

which "the call-note, whit, and the ordinary song, se-bic', are repeated many times." Chapman's (1932:372) description of "crescendo passages" in which the male "literally rises to the occasion, and on trembling wings sings an absurd chebéc, tooralooral, chebéc, tooral-ooral" is puzzling. One hardly knows whether this is a flight song or not. I certainly have never heard such a song, though on two occasions during the early part of the incubation period a male on approaching the nest gave a series of flight-notes and *che-bec* phrases run together: and on another occasion, when adult flycatchers were defending one of their young against a Chipmunk (Tamias striatus), they gave a jumbled mixture of notes none of which sounded quite familiar. A well defined flight song which I witnessed at 7:30 p.m. on July 3, 1946, was performed 75 feet overhead. Hearing continuous che-bec song above me, I looked up, searched the sky, and saw a Least Flycatcher making short dips in its flight over the forest. Suddenly both song and flight ended as the bird closed its wings and dived straight down to the woods. While this song lasted, no other Least Flycatcher in the area was singing.

Evening Song. The above-described flight song is the only well defined song I have ever heard a Least Flycatcher sing in the evening. The male sings no evening twilight song in any way comparable to the morning song, though of course he may utter an occasional *che-bec* as he does otherwise during the day. The Wood Pewee often sings a twilight song in the evening.

Call notes of the female. The female does little, if any, true singing. She moves about the nest quietly. Occasionally she calls whit while feeding or as the male approaches and leaves the nest. She sometimes gives an extended series of chweep-notes. If this chweep is a song-note at all comparable to the male's che-bec, it differs in that it is softer and wholly unaccented at the end. I found that I could distinguish the female from the male on the basis of this note. Both the male and female called whit, of course, but only the male called che-bec, and only the female called chweep.

The female used her *chweep*-note in defending the nest against various animals, notably man. I observed a female fly off from a nestful of young when a Thirteen-lined Ground Squirrel (*Citellus tridecemlineatus*) came to the foot of the nest-tree. She attacked furiously, the outburst of *chweep*-notes lasting until the rodent departed. She gave a series of *chweep*-notes in the nest-tree before she returned to the nest and settled down to brooding. The male was nowhere to be seen, and did not return for some time.

SUMMARY

In the vicinity of Douglas Lake, Michigan, the Least Flycatcher's principal nesting habitat is more or less open second-growth aspen associes. Of 44 nests studied in 1942, 1944, and 1946, 20 were along the very edges of clearings, 18 were less than ten feet from the edges, and 6 were slightly more than 20 feet back from the edges. The population density of favored habitat (i.e., aspen

woods intersected by roads and paths) was 200 to 271 pairs per 100 acres; that of unbroken aspen woods, not far away, 70 pairs per 100 acres.

The territories of the 44 pairs studied were of two sorts: (1) that in which a pair mated, nested and fed throughout the whole reproductive cycle, and (2) that in which a pair mated and nested, but fed in a neutral or communal feeding area adjoining. These neutral feeding areas were not defended. Nest territories varied in size from .5 acres to .03 acres (average of 33 measured territories: .18 acres). Territories were defended principally by the males, their singing being an important means of advertisement, defense and maintenance. The male's morning song began before dawn and ended about sunrise. It was a continual repetition of the phrase che-bec. When most fervent (just before sunrise early in the incubation period) it was repeated about 60 times per minute. Daytime song was desultory and sometimes followed territorial dispute. A flight song, performed in the evening 75 feet above the ground, was a rapid repetition of che-bec phrases. I heard no twilight evening song at all comparable to the twilight morning song. Throughout that part of the reproductive cycle which I observed (egg-laving to the scattering of the young), males devoted a definite part of each morning to singing.

During three visits of a pair of Cedar Waxwings which destroyed a Least Flycatcher nest in stealing material from it, the male flycatcher did not attack until the waxwings were at the nest, and the female flycatcher remained in the nest (which she defended to some extent by pecking) until the final visit, when the nest was pulled completely loose from its moorings. She then joined the male in aerial, but futile, attack.

There seemed to be no friction between Least Flycatchers and such Wood Pewees, Crested Flycatchers, Phoebes and Kingbirds as nested in the vicinity.

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NEW LIFE MEMBER



Aaron Moore Bagg was born at Holyoke, Massachusetts on April 6, 1912, son of Aaron Clark Bagg and Helen Moore Bagg. As a child he was privileged to have the Duck Hawks of Mt. Tom as avian neighbors, and to gaze upon that priceless possession of the household—a watercolor portrait of a Duck Hawk by Louis Agassiz Fuertes. He attended Hotchkiss School and in 1934 obtained his bachelor's degree from Princeton, A newspaper writer by profession, he is an enthusiastic amateur ornithologist, being an Associate of the American Ornithologists' Union and a member of the Massachusetts and New Hampshire Audubon Societies. He is especially interested in hawk flights and has published thought-provoking papers concerning the correlation between barometric pressure-patterns and spring bird migrations. With Henry M. Parker he has been making a special study of the northward spread of the Turkey Vulture into New England. He became a member of the Wilson Ornithological Club in 1948. He is now serving as a trustee of the organization.